

AN UNUSUAL OSTEOLEPIFORM FISH FROM THE LATE DEVONIAN OF VICTORIA, AUSTRALIA

by J. A. LONG

ABSTRACT. A new osteolepiform fish, *Beelarongia patrichae* gen. et sp. nov., is described from the Late Devonian (Frasnian) lacustrine Mount Howitt site, eastern Victoria. *Beelarongia* is cosmine-covered, has a broadly flaired parietal shield with large extratemporal bones, cheek plate with an additional small postorbital bone and broad lateral extrascapulars. The orbits are very small. The scales are rhombic with high dorsal processes. *Beelarongia* is considered closely related to *Canowindra grossi* Thomson because of the shape of the parietal shield, presence of an accessory postorbital bone behind the small orbit, and broad extrascapular series.

UNTIL recently almost our entire knowledge of the osteolepiform fishes was based on studies of material from the Northern Hemisphere which formed part of the Laurasian landmass in mid-Palaeozoic times. New discoveries from Australia and Antarctica, which formed East Gondwana, or the antipodes to Laurasia during the Devonian, reveal a diverse osteolepiform fauna, some elements of which are unexpectedly different from the Northern hemisphere faunas. Aside from fragments attributed to *Strepsodus* by Woodward (1906) the first fossil crossopterygian described from Australia was *Canowindra grossi* Thomson (1973) from the Upper Devonian Mandagery Sandstone of New South Wales. Thomson described the single complete fish from a natural mould, but was uncertain how to classify it. Since then Long (1985b) has redescribed *Canowindra* from new preparation of the original specimen, and regards it as an osteolepiform which is representative of a new higher taxon. Young and Gorter (1981) described ?*Gyroptychius* cf. *G. australis* from the Middle Devonian Hatchery Creek fauna, New South Wales, and Long (1985a) described a primitive eusthenopterid, *Marsdenichthys longioccipitus*, from the Late Devonian Mount Howitt locality, Victoria. Other osteolepiforms from Australia include *Gogonasus andrewsi* from the Upper Devonian Gogo Formation, Western Australia (Long 1985c) and new species of *Megalichthys* from the Lower Carboniferous of Queensland (Long and Turner, 1984). In August 1986 a complete skull of *Gogonasus* was discovered at Gogo and this material is currently under study. The new form described here is significant in that it shares several distinctive characters with *Canowindra*, and together with another undescribed form from the Middle Devonian of Antarctica may represent an endemic Gondwanan group of Osteolepiformes. In this paper the Mount Howitt form is described in detail. The erection of higher taxonomic ranks will be postponed until all the new material is fully described.

The material of *Beelarongia* was collected in the original excavations of the Mount Howitt site over the 1970/1 field seasons by Professor Jim Warren (Monash University, Zoology Dept.). As most of the bone was weathered away the pieces of cranium were recognized as natural impressions in the black shale and assembled together as best possible despite the absence of some pieces. The specimen was then cast with latex. All of the pieces are thought to belong to the one individual, although as they were found separately throughout the collection it cannot be determined exactly when they were found and if they came from the same horizon.

Terminology for dermal bones used herein follows Jarvik (1980) as discussed in Borgen (1983). The words 'breadth, length, and height' are abbreviated as L, B, and H respectively. All measurements were taken across the surface of bones, thus incorporating some degree of flattening where present. Indices are expressed as the product of two linear dimensions multiplied by 100.

SYSTEMATIC PALAEONTOLOGY

Order OSTEOLEPIFORMES (OSTEOLEPIDIDA)

Remarks. Despite recent arguments that the Osteolepiformes could be a paraphyletic group (Rosen *et al.* 1981; Lauder and Liem 1983; Gardiner 1980), I have presented arguments that the group is probably monophyletic (Long 1985a), but admit that the evidence for this hypothesis is scarce. Osteolepiform fishes uniquely possess a pectoral girdle with a large ornamented anocleithrum separating the cleithrum from contact with the supracleithrum. There are large basal scutes present at fin bases (Andrews 1973). The cheek has a bar-like preopercular bone which forms the rear border to the single, large irregularly-shaped squamosal, and is steeply inclined. The squamosal is unique amongst Osteichthyes in occupying most of the cheek plate area and having six sides of which five suture to other cheek bones. This character also applies to some early tetrapods which are here regarded as a subgroup of the Osteolepiformes, probably of close affinity to the Panderichthyidae (Schultze 1970; Schultze and Arsenault 1985) and not immediately related to the Dipnoi as suggested by Rosen *et al.* (1981). The only group of Osteolepiformes in which cheek patterns may be confused with those of tetrapods is the panderichthyids (Schultze and Arsenault 1985). The cheeks of panderichthyids are poorly known. They differ slightly from those of other osteolepiforms in contact margins between the lachrymal and jugal (*Elpistostege*) and in having a slightly smaller lachrymal (*Panderichthys*). In the primitive labyrinthodonts which retain an osteolepiform-like cheek pattern (*Ichthyostega*, *Acanthostega*, *Crassigyrinus*) the preopercular is much reduced and the jugal has become much larger than the squamosal (Jarvik 1980; Panchen 1973, 1985).

Beelarongia gen. nov.

Etymology. From the aboriginal word 'beelarong' meaning shiny (Reed 1975), an allusion to the cosmine covered dermal bones and scales.

Diagnosis. A presumably cosmine-covered osteolepiform with a fronto-ethmoid shield/parietal shield ratio of approximately 80; index of lengths of frontal/parietal bones about 60. Parietal shield anteriorly narrow but posteriorly broad with a B/L index of 180, posterior margin strongly pointed posteriorly. Extratemporal very large, being almost one third as broad as one side of the parietal shield. Median extrascapular having a short anterior margin, one fifth the extent of that of the broad lateral extrascapulars. Cheek with long postorbital and one small accessory postorbital bone. Orbits very small. Opercular large, rounded. Cleithrum with broad unornamented anterior flange. Scales rhombic with large dorsal processes.

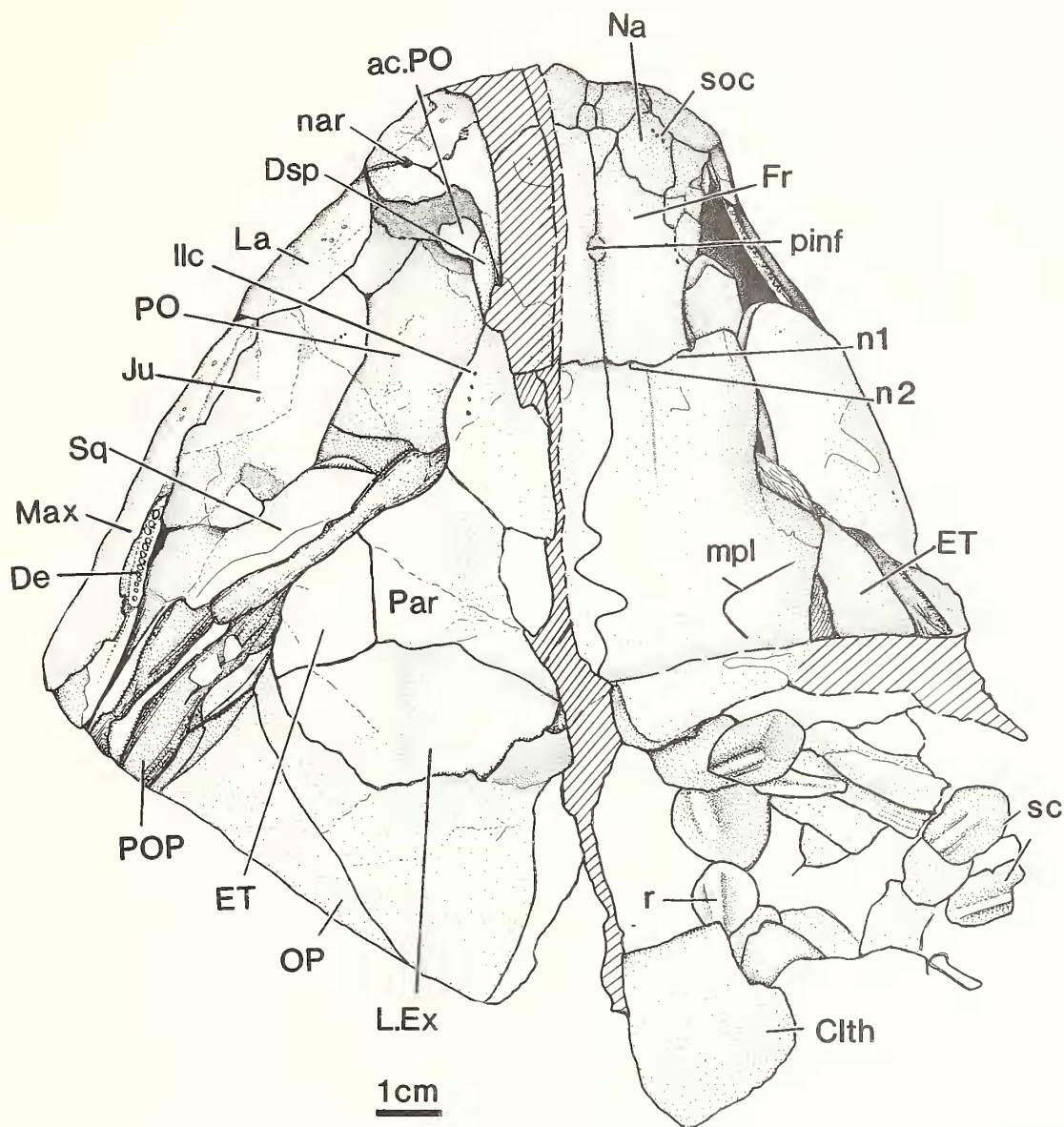
Remarks. *Beelarongia* is distinguished from all other osteolepiforms, except *Canowindra*, by its very small orbits which have a small accessory postorbital bone behind them, the unusually large extratemporal bones and very broad posterior division on the parietal shield. It is distinguished from *Canowindra*, which also has the above features, by the presumed presence of cosmine, narrower shape of the extratemporal bones, the rhombic scales with high dorsal processes, and the simpler cheek pattern with only one accessory postorbital bone (*Canowindra* has two accessory postorbitals, Long 1985b). Cosmine is presumed to be present on *Beelarongia* because of the smooth surface of the bones and scales from the natural mould. The thick rhombic scales of *Beelarongia* are almost identical to those of other cosmine-covered osteolepiforms.

Type species. *B. patrichae* sp. nov.

Beelarongia patrichae sp. nov.

Plate 91; text-figs. 1-5, 6b

Etymology. After Dr Pat Rich (Monash University, Earth Sciences Dept.) who has given me much assistance and encouragement.



TEXT-FIG. 1. *Beelarongia patrichae* gen. et sp. nov., sketch of holotype NMV P160872, cranium in dorsal view. The rest of the specimen, containing most of the left opercular and pectoral girdle is not shown here. Cross hatching indicates damaged areas filled in by latex. ac.PO, accessory postorbital; Clth, cleithrum; De, dentary; Dsp, dermosphenotic; ET, extratemporal; Fr, frontal; Ju, jugal; La, lachrymal; L.Ex, lateral extrascapular; llc, main lateral line canal pores; Max, maxilla; mpl, middle pit-line groove; Na, nasal; nar, external nostril; n1, n2, notches on posterior margin of frontal; OP, opercular; Par, parietal shield; pinf, pineal foramen or elevation; PO, postorbital; POP, preopercular; r, basal ridge of scales; sc, scales; soc, supraorbital sensory-line pores; Sq, squamosal.

Holotype. NMV P160872 (Pl. 91), an almost complete head preserved as a natural mould in dorsal view, with part of the pectoral girdle and fin attached. Housed in the Museum of Victoria, Melbourne (NMV).

Material. NMV P160873, an isolated section of scales with part of a fin attached; NMV P160874, part of the squamation, and NMV P160875, cleithrum and clavicle.

Occurrence. From the lower mudstone outcropping along the Howqua River at the base of Mount Howitt (Marsden 1976); Avon River Group, Late Devonian (Frasnian, Long 1983).

Diagnosis. As for genus, only species.

Description. *Beelarongia* was a moderate-sized osteolepiform having an estimated maximum cranial length of 100 mm from the single known skull. The shape of the head can be easily determined from the holotype, being broad posteriorly but rapidly narrowing anteriorly, and quite depressed in cross-section. The sections of body squamation give no indication of the body shape or the disposition of the fins.

Fronto-ethmoid shield. The fronto-ethmoid shield is approximately as broad as long, with the dorsal face being flat posteriorly, arching convexly at the rostral margin (text-figs. 1 and 2). Few bones can be distinguished due to the poor preservation. The large frontals are separate from the other bones forming the shield, with a distinct concave lateral margin on the right frontal for the dermosphenotic. The supraorbital canal is assumed to run off the frontal to the dermosphenotic, indicated on the specimen by a series of fractures where the canal would be expected. Approximately halfway along the median suture between the frontals there is a median rough area on the cast; this is either a pineal thickening or a foramen (pinf).

The frontals (Fr) comprise three quarters of the estimated length of the fronto-ethmoid shield, being about twice as long as broad. In the right frontal a row of pores representing the supraorbital canal (soc) can be seen close to the rostral margin. The posterior margin of the fronto-ethmoid shield has an irregular shape with two notches (n1, n2) present on the margin of the right frontal (text-fig. 1), possibly for ligaments as Jarvik (1972) has suggested for similar notches in the fronto-ethmoid shield of *Glyptolepis*. The dermosphenotic (Dsp) is seen on the left side, displaced from the skull roof table to lie next to the postorbital (text-figs. 1 and 2). It is almost rhombic in form with rounded margins, comprising three quarters the length of the frontals and is half as broad as long. The mesial margin is smoothly convex to fit into the frontal, but the lateral margin is straighter with a long posterior division contacting the postorbital and a short anteromesially directed anterior side for the supraorbital. The dermosphenotic has an extensive overlap surface for the anterior part of the postorbital (oa.Dsp, text-fig. 2b) indicating that the cheek was firmly attached to at least the anterior division of the skull.

An indistinct foramen, possibly the nasal opening (nar), is visible on the left side of the fronto-ethmoid shield (text-figs. 1 and 2A). It is an almost circular opening situated just anterior to the lachrymal as in other osteolepiforms. The orbital notch is not clearly defined on the fronto-ethmoid shield. The close proximity of the bones surrounding the orbit, and the reconstruction of these bones in the articulated cheek indicate that the orbits of *Beelarongia* were very small, similar to those of porolepiforms in being even smaller than those of small-eyed osteolepiforms such as *Glyptopomus* (Jarvik 1950) or *Latvius* (Jessen 1966, 1973).

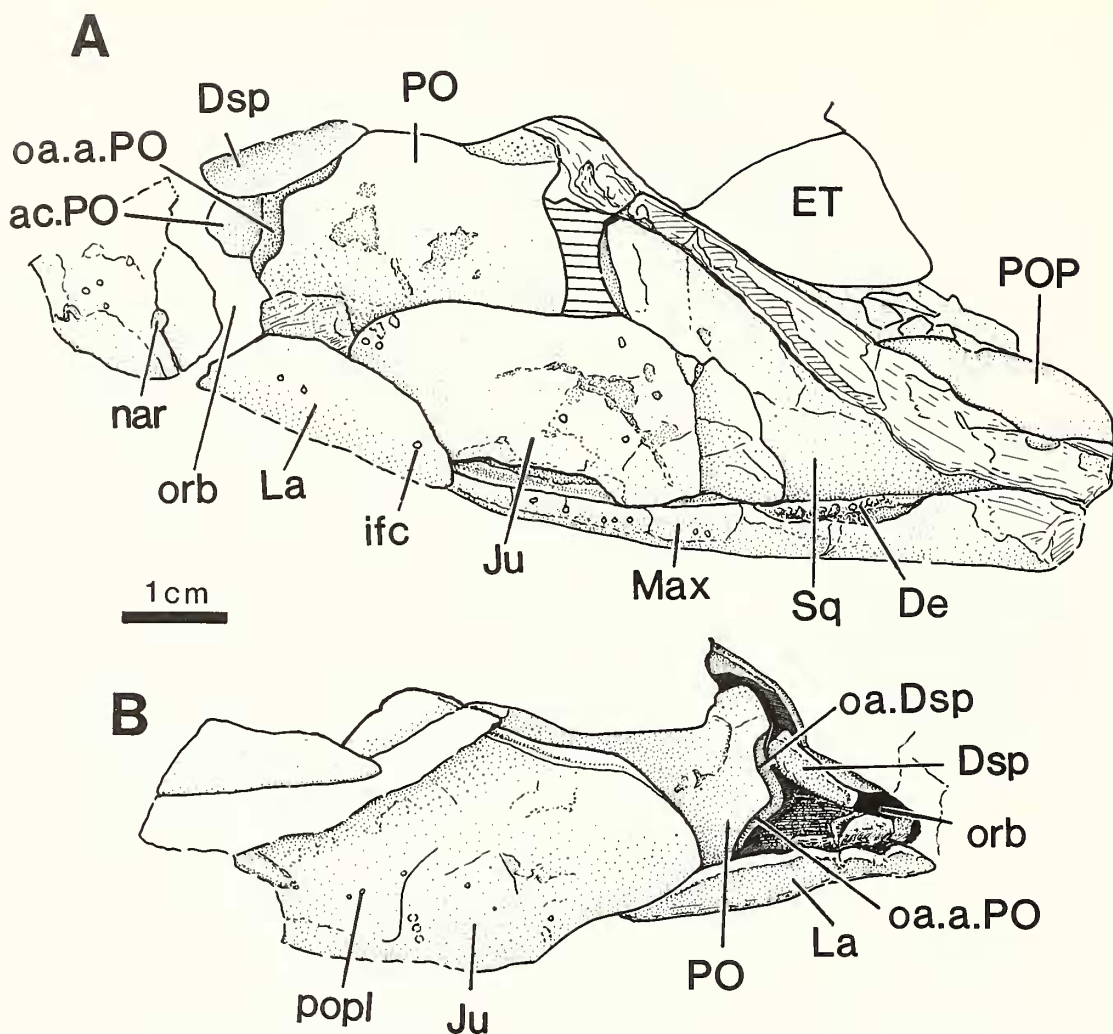
Parietal shield. The parietal shield is well preserved although only the extratemporal bones (ET) are clearly differentiated from the rest of the cosmine-covered shield (Pl. 91; text-fig. 1). In cosmine-covered osteolepids the sutures between the parietal, intertemporal, and supratemporal are occasionally not visible (Jarvik 1948, 1985; Jessen 1966) but are distinct in forms which have no cosmine. The absence of such sutures in *Canowindra* is believed to reflect the actual condition of fusion between these bones rather than the sutures being merely masked by the external cosmine layer (Long 1985b). As *Beelarongia* is closely related to *Canowindra*, as discussed below, the condition of the parietal shield in *Beelarongia* is also thought to be similar to that of *Canowindra*. The overall shape of the parietal shield is similar to that of *Latvius grewingki* (Gross 1956, pl. 1), but differs in having an even broader posterior region with larger extratemporals. The posterior margin has two clearly defined angular notches, the first being just mesial to the extratemporal, the second being situated about midway along the

EXPLANATION OF PLATE 91

Figs. 1–3. *Beelarongia patrichae* gen. et sp. nov. 1, holotype cranium NMV P160872 in dorsal view. 2, cleithrum in lateral view with clavicle in ventrolateral view, NMV P160875. 3, part of the squamation showing scale with high dorsal process, NMV P160874. Latex casts whitened with ammonium chloride.



LONG, canowindridoid osteolepiforms



TEXT-FIG. 2. *Beelarongia patrichae* gen. et sp. nov., cheeks in lateral view, from holotype NMV P160875. A, left cheek. B, right cheek. Parts of the dorsal edge of the cheek were not well preserved and did not cast very well. Abbreviations as for text-fig. 1 except for: ifc, infraorbital sensory-line canal pores; oa.a.PO, overlap area for accessory postorbital bone; oa.Dsp, overlap area for dermosphenotic; orb, orbit; popl, preopercular sensory-line canal.

margin. These notches are also seen on *C. grossi* and a few other osteolepiforms (*Thursius moythomasi*, Jarvik 1948, pl. 19; *Gyroptychius dolichotatus*, Jarvik 1985, fig. 12). The anterior margin of the parietal shield is not completely shown in the specimen, but is assumed to have an irregular form to comply with the notches for ligamentous attachments seen on the posterior margin of the fronto-ethmoidal shield. The lateral margins of the parietal shield are smoothly curved with a strong median concavity before splaying out laterally near the contact with the extratemporal. The parietal suture courses in an irregular zig-zag fashion close to the posterior margin. The transverse (middle) and posterior parietal pit-lines are situated close to the posterior margin of the shield, meeting at a point slightly closer to the extratemporal than to the median suture.

The extratemporal (ET) is a large, triangular bone approximately as long as broad. It is a third as long as the parietal shield and almost a third as broad as one half of the shield. The mesial and posterior margins of the extratemporal are almost straight, but the lateral margin is strongly convex. Although the shape of the extratemporal is similar to that of several other osteolepiforms, most of which have a high degree of variation in

the shape of that bone (e.g. *G. dolichotatus*, Jarvik 1985, fig. 12) none of the described forms approach *Beelarongia* or *Canowindra* in the proportional size of the extratemporal to the rest of the parietal shield. *Porolepis* has a similarly sized extratemporal but differs in the shape of this bone, which is more elongated (Jarvik 1972).

Extrascapulars. The left lateral extrascapular (L.Ex) is preserved on the holotype. The imperfect bone preserved on the right side which shows an overlap surface is not the right lateral extrascapular but part of the right opercular which has been displaced over the rear of the skull roof. Overlap relationships are not known for the extrascapulars, although it may be noted that in *Canowindra* there is normal osteolepiform overlap of the median bone by the lateral extrascapulars. The lateral extrascapular is a large rounded bone which is about one and a half times as broad as long. The anterior margin is strongly convex with two angular prominences. The lateral margin, considerably shorter than the mesial margin, is gently convex (Pl. 91A). The median extrascapular would have been very narrow at its contact with the parietal shield. There is no indication of the course of the main lateral line canal or the occipital canal on the material.

Cheek. The cheek of *Beelarongia* is well preserved on the left and part of the right side of the holotype (text-figs. 1 and 2). The anterior division is poorly known because of post-mortem collapse of the bones around the orbit. It is clear that the normal pattern of cheek bones was present: squamosal (Sq), jugal (Ju), postorbital (PO), lachrymal (La), preopercular (POP), and probably the quadratojugal although this is not seen in the material. The posterior region of the cheek is not at all well preserved, but part of the preopercular is preserved on the left side of the specimen. The infraorbital series of *Beelarongia* differs from that of most osteolepiforms in that the lachrymal is quite smaller and narrower than the jugal and postorbital elements (text-fig. 6).

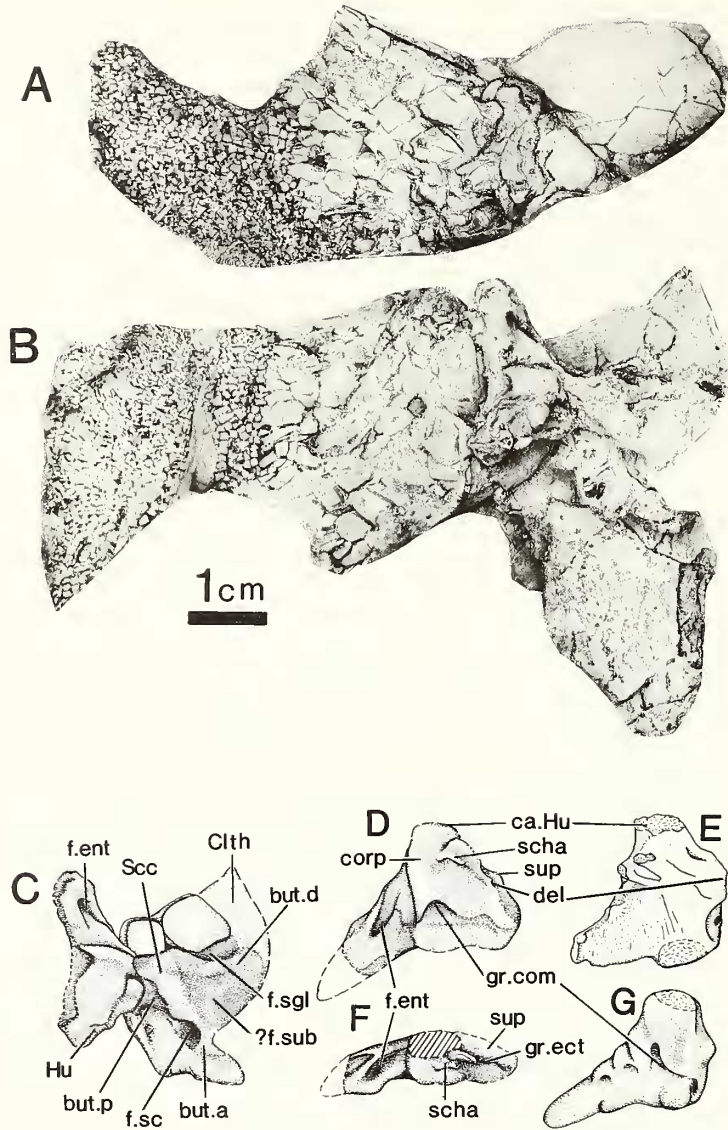
The lachrymal can be seen on both sides of the holotype immediately ventral and posterior to the orbit. It is two thirds the length of the jugal, and slightly more than half as long as the fronto-ethmoid shield. The dorsal margin is not well preserved on either of the two examples, presumably fitting below the orbit, but not necessarily participating in the orbit. Open pores of the infraorbital canal are visible close to the ventral margin of the lachrymal.

The jugal is a large bone contacting the lachrymal anteroventrally, the postorbital dorsally, the squamosal posteriorly and the maxilla ventrally. The anterior contact is obscure, as if the bones are placed in approximate juxtaposition there is a space immediately posterior to the orbit for a small accessory postorbital bone. This is further supported by the anterior margin of the postorbital which shows a broad overlap flange for another dermal element (text-fig. 2A). There is a small area of bone preserved anterior to the postorbital which is identified as the accessory postorbital (ac.PO, text-fig. 2A). This bone is a small almost square plate which corresponds in size to the anterior accessory postorbital of *Canowindra*, but differs markedly from that element in *Canowindra* by its shape. However, it is alternatively possible that this small bone in front of the postorbital is part of the supraorbital which has fallen down from the skull roof. In view of the anterior overlap area on the large postorbital and the general fit of the bones around the orbit it is most likely that an additional postorbital element is indeed present, as restored in text-fig. 5. The jugal has an elongate form, being slightly more than twice as long as high. The dorsal margin is gently curved, turning steeply at the anterior margin to form an anterior point. The posterior margin is strongly convex, curving downwards to meet the straight ventral margin. There are numerous pores present indicating the presence of the preopercular sensory line, although its exact course and junction with the infraorbital canal are not clear.

The postorbital (text-figs. 1 and 2) is a large bone dorsal to the jugal, lateral to the dermosphenotic and anterior to the squamosal. It is unusual in having a broad anterior end with two overlap flanges, a dorsal one for the dermosphenotic (oa.Dsp) and a ventral flange for an additional small accessory postorbital bone (oa.a.PO), as also occurs in *Canowindra* in which two accessory postorbitals are found (Long 1985b). The anterior part of the dorsal margin is relatively straight, but moderately inclined anteroventrally; the anterior margin being pointed with a concave facet bearing broad overlap surfaces on either side of the point. The posterior margin is indented for overlap of the squamosal. Overall the postorbital is slightly longer than high, and marginally shorter than the jugal.

The anterior region of the squamosal (Sq) is preserved on both sides of the specimen (text-fig. 2). The anterior margin has a dorsal pointed division for contacting the postorbital and a smoothly concave ventral division for the jugal. From the extent of the whole cheek, restored by the relative position of the opercular and fronto-ethmoidal shield, the squamosal was particularly large relative to the other cheek bones, a character typifying the osteolepiforms.

The dorsal region of the preopercular can be seen on the left side of the specimen. All that can be said about this bone is that it was situated right at the rear of the cheek complex with a steeply inclined long axis as in other osteolepiforms.

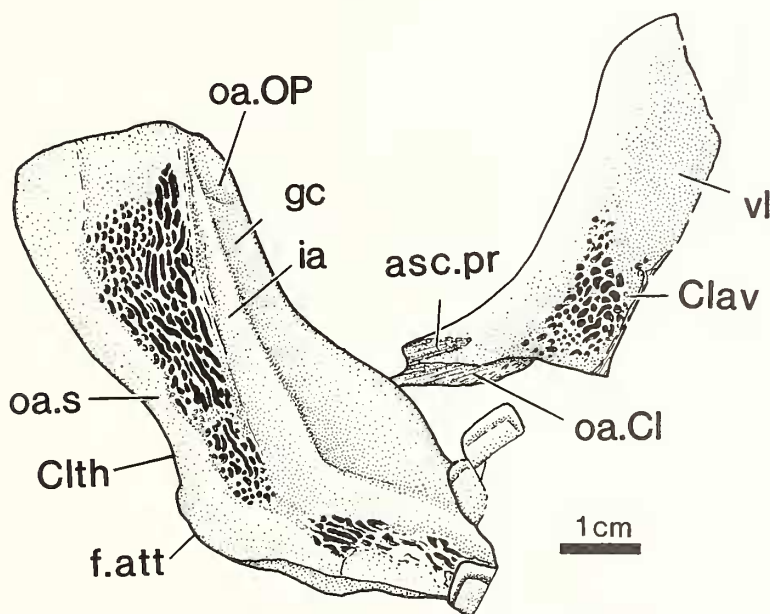


TEXT-FIG. 3. *Beelarongia patrichae* gen. et sp. nov., left pectoral girdle and fin, from the holotype NMV P160875. A, external view of fin, counterpart to B, internal view of cleithrum showing scapulocoracoid and humerus. C, sketch interpretation of scapulocoracoid and humerus as preserved. D, F, attempted restoration of the humerus in (D) ventral and (F) anterior views. E, left humerus of *Sterropterygion* in ventral view (after Rackoff, 1980). G, left humerus of *Eusthenopteron* in ventral view (after Jarvik, 1980). but.a, but.d, but.p, anterior, dorsal and posterior buttress of scapulocoracoid; ca.Hu, caput humeri; Clth, cleithrum; corp, corpus of humerus; del, crest for deltoideus muscle; ent, entepicondyle; f.ent, entepicondylar foramen; f.sc, supracoracoid fossa; f.sgl, supraglenoid foramen; ?f.sub, area of subscapular fossa; gr.com, commissural groove; gr.ect, ectepicondylar groove; scha, shelf for attachment of scapulohumeroideus muscle; sup., ridge for supinator muscle; Scc, medial division of the scapulocoracoid.

Operculogular series. The opercular bone (OP) is the only element of this series preserved on the specimen, being almost completely preserved on the left side. Text-fig. 1, which shows part of the opercular, does not show that part of the specimen which joins onto the opercular as this contains the pectoral girdle and cannot be properly studied if glued back to the block containing the cranium. The opercular is subrectangular in shape with an estimated B/L index around 112 (restoring the dorsal margin). The anterior margin is straight and comprises 54% of the opercular length in its extent. The dorsal margin is not preserved, but can be restored to fit the posterolateral margin of the skull table. This gives a deeply concave dorsal margin. The posterior margin is strongly convex, curving smoothly round to the ventral margin without a marked posteroventral corner developed.

Pectoral girdle and fin. The holotype shows the proximal region of the left pectoral fin and shoulder girdle preserved (text-fig. 3), and NMV P160875 shows the external surfaces of the cleithrum and clavicle well preserved (Pl. 91; text-fig. 4). It should be noted that the left pectoral girdle and fin attach to the side of the skull in text-fig. 1, completing the posterior region of the opercular and showing the humerus and scapulocoracoid resting inside the flattened cleithrum.

The cleithrum (Clth; text-figs. 1, 3, 4) has a large dorsal rectangular division which is slightly more than twice as long as the ventral triangular division (dividing line taken as the line passing through the broadest section of the bone). The externally exposed ornament is restricted to a narrow triangle on the dorsal rectangular division, occupying less than half of the surface area. The dorsal margin is straight, and the anterodorsal corner has a depressed curved area for the overlap of the opercular (oa.OP). The posterior margin has a slightly concave dorsal division with a well rounded bulge for the scapulocoracoid where the pectoral fin inserted (f.att). The inwardly bent smooth area anterior to the ornament has a broad outer region (ia), probably for the membranous cover of the posterior wall of the branchial cavity (Jarvik 1948, p. 98) and a slightly narrower inner strip which was presumably covered by soft tissues at the rear of the gill cover (gc). The visceral surface of the cleithrum is partially



TEXT-FIG. 4. *Beelarongia patrichae* gen. et sp. nov., cleithrum in lateral view with associated clavicle in ventrolateral view, NMV P160875. asc.pr, ascending process of clavicle; Clav, clavicle; Clth, cleithrum; f.att, area where pectoral fin attaches to scapulocoracoid; gc, inner smooth lamina of cleithrum forming part of the gill chamber; ia, inner smooth area of cleithrum; oa.Cl, overlap area for cleithrum; oa.OP, overlap area for opercular; oa.s, overlap area for scales; vl, ventral lamina of clavicle.

preserved on the holotype, being smooth and featureless aside from the endoskeletal attachment area, hidden on the specimen by the scapulocoracoid (Sec). In having a relatively short ventral triangular division the cleithrum of *Beelarongia* is typical of osteolepiforms, although the development of a broad, smooth, inwardly bent area on the external surface is a feature of porolepiform cleithra (Jarvik 1972, p. 125).

The clavicle (Clav) is partially preserved on NMV P160875 (text-fig. 4). It has an ascending process (asc.pr) with a distinct overlap flange for the cleithrum (oa.Cl), and features a broad ventral lamina (vl). In overall length it approaches that of the cleithrum (noting the absence of the tip of the ascending process). The dorsolateral vertical portion of the clavicle is a narrow, smooth region which meets the ventral, ornamented wall along a pronounced lateral ridge.

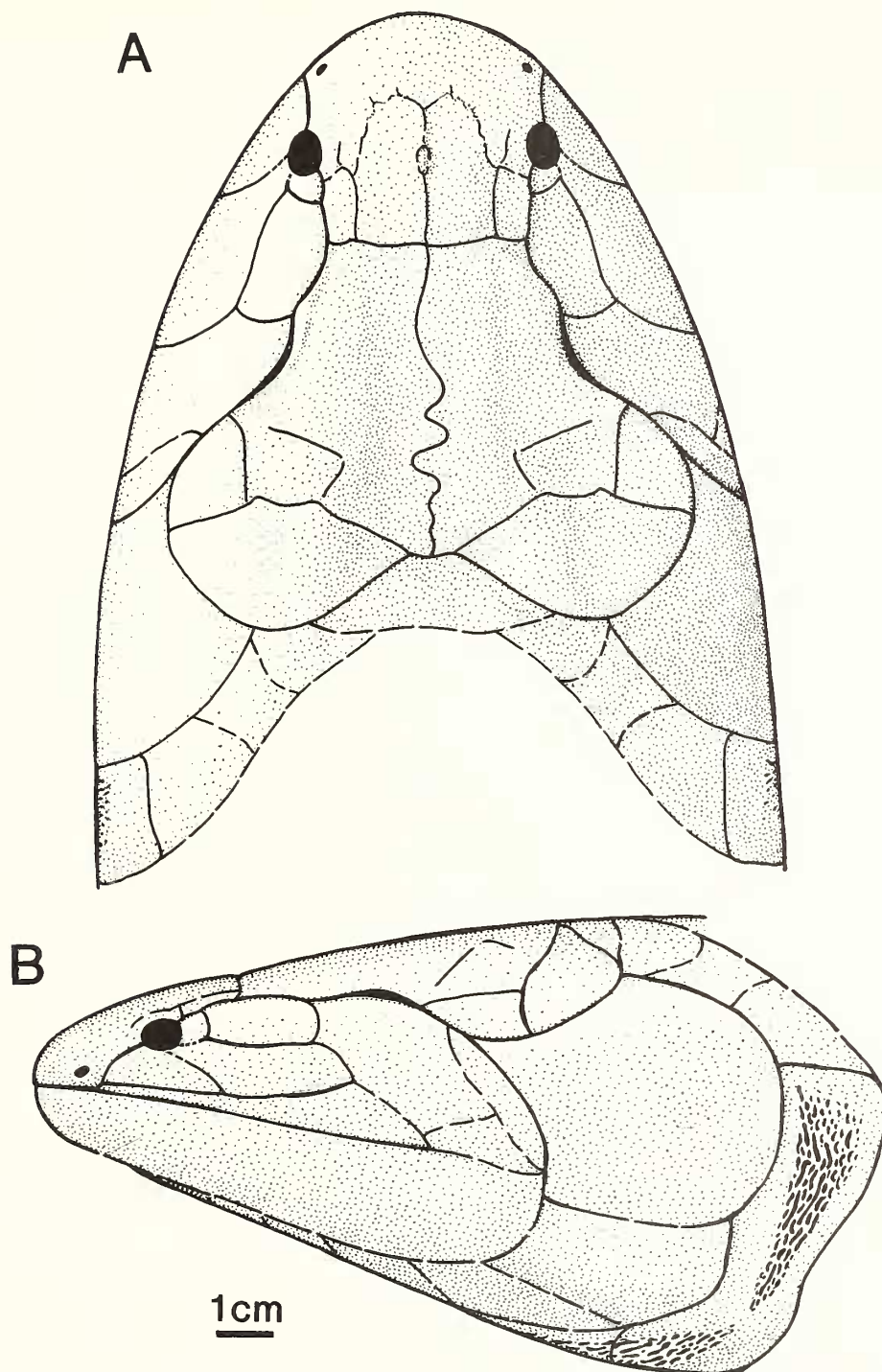
The scapulocoracoid (Sec) and humerus (Hu) are poorly preserved inside of the left cleithrum. In general form the scapulocoracoid (text-fig. 3C) is elongate, being just under half as broad as long, and slightly broader than deep (height relative to mesial wall of cleithrum). The mesial or visceral surface is quite flat, merging smoothly forward to meet the mesial wall of the cleithrum, although as it is studied from a latex cast the exact nature of the subscapular fossa (?f.sub) cannot be determined. There appears to be anterior (but.a) and dorsal buttresses (but.d) supporting the central body of the scapulocoracoid, as in other osteolepiforms (Andrews and Westoll 1970a, 1970b; Janvier 1980), although the space between the posterior buttress (but.p) and the wall of the cleithrum is not differentiated on the latex cast. At the point where the humerus meets the scapulocoracoid, at the glenoid fossa, the mesial surface of the scapulocoracoid is most furthest from the inner surface of the cleithrum. Both the supracoracoid foramen (f.ssc) and supraglenoid fossa (f.sgl) are seen. Overall the scapulocoracoid of *Beelarongia*, as far as can be described, conforms to the usual osteolepiform type, but may differ in the absence of a well-developed subscapular fossa if this absence is not an artifact of latex casting, as may be the case here.

The humerus (Hu, text-fig. 3C, D, F) can be seen to be a broad bone, more than twice as broad as the long axis of the shaft, as preserved, but probably much broader as the entepicondylar process is incomplete. To facilitate comparisons I have figured the humeri of two other osteolepiforms (text-fig. 3E, G) in which it is well known: the osteolepid, *Sterropterygion* (Rackoff 1980), and the eusthenopterid, *Eusthenopteron* (Andrews and Westoll 1970a; Jarvik 1980). The distal surface is not well preserved on the specimen as it is covered by scales of the fin web which reach high up on the fin-lobe. In overall form the humerus is similar to that of *Eusthenopteron* (text-fig. 3G) in the long entepicondyle (ent.) and well defined commissural groove (gr.com). Processes for attachment of the scapulohumeroideus (scha), supinator (sup), and deltoideus (delt.) muscles are present, but the latter two are not as well developed as on the osteolepid *Sterropterygion* (text-fig. 3E). The deltoideus crest is seen as a small bump separated from the dorsal side of the humerus which bears the supinator muscle ridge by a well formed groove (text-fig. 3F). The entepicondylar foramen (f.ent) is a deeply excavated pit seen on the ventral surface of the entepicondyle. This differs from the condition in both *Sterropterygion* and *Eusthenopteron*. In *Eusthenopteron* the entepicondylar foramen or canal runs almost parallel with the corpus of the humerus to open posteriorly near the articulatory facet for the ulna, and in *Sterropterygion* the entepicondylar foramen is either not noticeable or absent (Rackoff 1980, figs. 5 and 6). This major difference in the morphology of the humerus indicates a possible early differentiation of the pectoral fin of *Beelarongia* from that of other osteolepiforms.

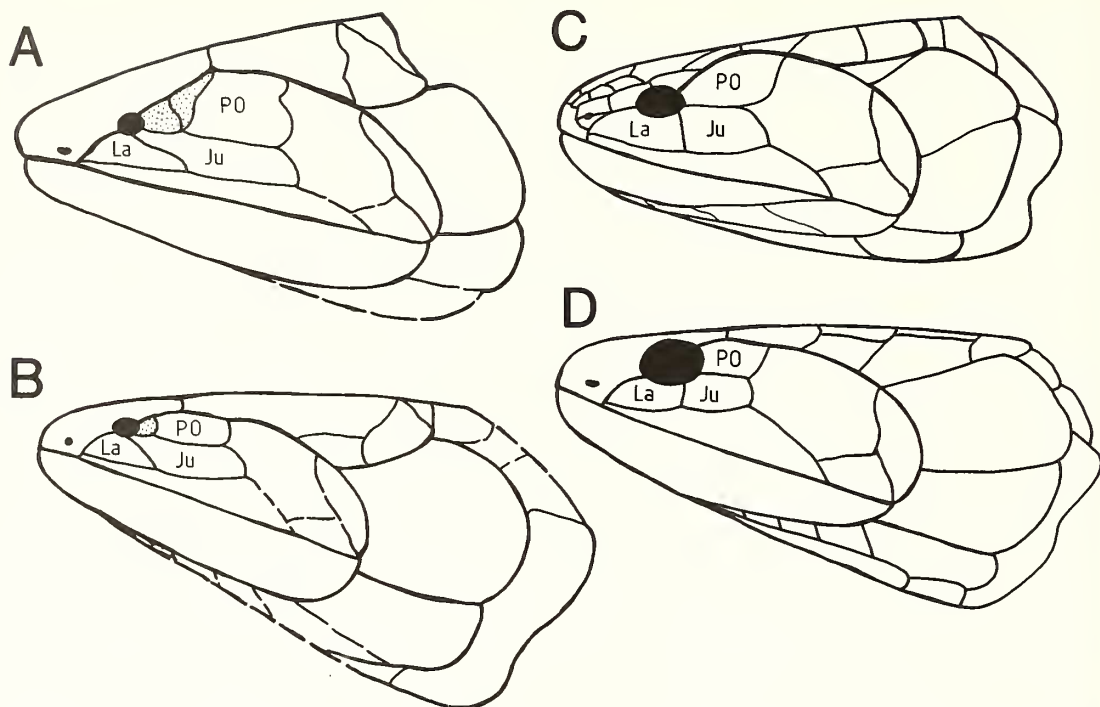
The proximal region of the pectoral fin can be seen on the holotype (text-fig. 3A, B). The scale covered lobe is short, relative to cranial length, as in osteolepiforms (although it should be noted that the length of the pectoral fin is unknown for other primitive 'crossopterygians' such as *Porolepis*, *Powichthys*, or *Youngolepis*; Jarvik 1972; Jessen 1980; Chang 1982). Lepidotrichia (f.r) are segmented and bifurcation occurs only once in the preserved area. Each lepidotrichial segment has a rectangular cosmine face separated from the cylindrical basal bone by a restricted neck.

Scales and squamation. There are a few specimens showing the scale morphology and parts of the intact squamation (holotype, NMV P160873, P160874; Pl. 91, fig. 3; text-fig. 1) but none of these specimens have the bone preserved well enough to show histological structure.

The typical flank scales are rectangular, being about three-quarters as long as deep. The thick cosmine covered external surface has a narrow groove running parallel to the dorsal and anterior margins for an interlocking fit with the overlapping scales. The dorsal end of each scale features a large process which is approximately one third as high as the whole scale, similar to the condition in palaeoniscoid scales. Anterior to the cosmine surface is a smooth overlap area equal to about one fifth of the scale breadth. The basal surface of each scale has a vertical thickening running parallel to the anterior margin and a large depressed area in the ventral half of the scale for receiving the dorsal process of the scale below. Scales covering the pectoral fin are rhombic, decreasing in size distally from the fin base. Along the leading edge of the fin there is an elongated narrow basal fin scute. Minute fin scales close to the junction with lepidotrichial rows are rectangular in form.



TEXT-FIG. 5. *Beelarongia patrichae* gen. et sp. nov. Attempted restoration of the head in A, dorsal view, and B, lateral view, after the holotype, NMV P160875.



TEXT-FIG. 6. Comparison of the heads in lateral view (A–D) of two closely related East Gondwana osteolepiforms (A, B) and two typical osteolepiforms (C, D). Accessory postorbital bones stippled. A, *Canowindra grossi* (after Long 1985b). B, *Beelarongia patrichae* gen. et sp. nov. C, the eusthenopterid *Eusthenopteron foordi* (after Jarvik 1980). D, the osteolepidid *Osteolepis macrolepidotus* (after Jarvik 1948). Abbreviations as for text-fig. 1.

The squamation is known from isolated blocks of scale impressions of uncertain position on the body. Scale rows are near-vertically disposed on the body, as seen close to the cranium and indicated by the angles of contact between externally exposed scale surfaces.

DISCUSSION

Within the Osteolepiformes *Beelarongia* shares the following features with *Canowindra grossi*: small orbits, parietal shield with a very broad posterior division, large extratemporal bones, possible fusion between the parietal–intertemporal–supratemporal bones, extrascapulars which are unusually broad and short, and an additional cheek element anterior to the postorbital bone (text-figs. 5 and 6A, B). The taxonomic distribution of these characters within the Osteichthyes has been discussed for *Canowindra* (Long 1985b) and this will not be reiterated here, except to say that on the basis of that work *Beelarongia* is here regarded as a sister taxon to *Canowindra*. Both *Beelarongia* and *Canowindra* are regarded as true osteolepiforms because of the nature of the cheek plate (having a single large squamosal, lacking a prespiracular bone behind the postorbital, no preoperculo-submandibular present, and bar-like preopercular which is steeply inclined to form most of the posterior margin of the cheek plate), the overlap relationships of the extrascapulars (median extrascapular overlapped by lateral extrascapulars), the presence of only one pair of external nares (known with certainty only in *Canowindra*), and in the structure of the shoulder girdle (large externally exposed anocleithrum, cleithrum with short ventral division). In addition *Beelarongia* has basal scutes, another characteristic feature of Osteolepiformes (Andrews 1973). The suggestion that *Beelarongia* and *Canowindra* are

closely related implies that the transition from rhombic to cycloid scales and the loss of cosmine in *Canowindra* occurred independently of other osteolepiform lineages.

Unfortunately we do not have information on the braincase or palate of these two interesting taxa, and lack of such data inhibits discussion of their relationships within the Osteolepiformes. Current views on osteolepiform interrelationships (e.g. Vorobyeva 1977) require revision in the light of recent discoveries (Long 1985c). Further remains of osteolepiforms which share derived characters with *Beelarongia* and *Canowindra* are now known from the Middle Devonian of Antarctica (Mount Crean fauna) and the Late Devonian of Victoria (South Blue Range fauna), supporting the suggestion (Long 1985b, 1985d) that these species probably belong to a new higher taxon of Osteolepiformes endemic to the East Gondwana Province (*sensu* Young 1981). The new material includes some preservation of the braincase and palate and, when described will enable further discussion of this problem.

Acknowledgements. Sincere thanks to Professor Ken Campbell (Geology Department, The Australian National University), Dr Peter Forey (British Museum of Natural History), and an anonymous referee for reading and commenting on the manuscript. Professor Jim Warren (Zoology Department, Monash University) allowed me to study the Mount Howitt material. Dr Gavin Young (Bureau of Mineral Resources, Canberra) is thanked for helpful discussion of the work. Dr Pat Rich (Earth Sciences Department, Monash University) supervised the first part of the work which formed part of a Monash University doctorate dissertation. The work was carried out at the Australian National University under the award of a Rothmans Fellowship, and at the University of Western Australia under a National Research Fellowship—Queen Elizabeth II Award.

REFERENCES

- ANDREWS, S. M. 1973. Interrelationships of crossopterygians. In GREENWOOD, P. H., MILES, R. S. and PATTERSON, C. (eds.). *Interrelationships of Fishes*, 137–177. Academic Press, London, New York.
- and WESTOLL, T. S. 1970a. The postcranial skeleton of *Eusthenopteron foordi* Whiteaves. *Trans. R. Soc. Edinb.* **68**, 207–329.
- 1970b. The postcranial skeleton of rhipidistian fishes excluding *Eusthenopteron*. *Ibid.* **68**, 391–489.
- BORGEN, U. J. 1983. Homologizations of exocranial roof bones between tetrapods and osteolepiform fishes. *Palaeontology*, **26**, 735–754.
- CHANG MEE-MAN. 1982. The braincase of *Youngolepis*, a Lower Devonian crossopterygian from Yunnan, south-western China. *Paps Dept. Geol. Univ. Stockholm*, 113 pp.
- GARDINER, B. G. 1980. Tetrapod ancestry: a reappraisal. In PANCHEN, A. L. (ed.). *The Terrestrial Environment and the Origin of Land Vertebrates*, 177–185. Academic Press, London and New York.
- GROSS, W. 1956. Über Crossopterygier und Dipnoer aus dem baltischen Oberdevon im Zusammenhang einer vergleichenden Untersuchung des Porenkanalsystems paläozoischer Agnathen und Fische. *K. svenska Vetensk-Akad. Handl.* **5** (6), 1–140.
- JANVIER, P. 1980. Osteolepid remains from the Devonian of the Middle East, with particular reference to the endoskeletal shoulder girdle. In PANCHEN, A. L. (ed.). *The Terrestrial Environment and the Origin of Land Vertebrates*, 223–254. Academic Press, London and New York.
- JARVIK, E. 1948. On the morphology and taxonomy of the Middle Devonian osteolepid fishes of Scotland. *K. svenska Vetensk-Akad. Handl.* **3** (25), 1, 1–301.
- 1950. On some osteolepiform crossopterygians from the Upper Old Red Sandstone of Scotland. *Ibid.* **2** (4), 1–35.
- 1972. Middle and Upper Devonian Porolepiformes from East Greenland with special reference to *Glyptolepis groenlandica* n.sp. *Meddr. Grönland*, **187**, 1–295.
- 1980. *Basic Structure and Evolution of Vertebrates*. Vol. 1. Academic Press, London and New York.
- 1985. Devonian osteolepiform fishes from East Greenland. *Meddr. Grönland., Geosci.* **13**, 52 pp.
- JESSEN, H. 1966. Die Crossopterygier des Oberen Plattenkalkes (Devon) der Bergisch-Gladbach-Paffrather Mulde (Rheinisches Schiefergebirge) unter Berücksichtigung von amerikanischem und europäischem *Onychodus*-Material. *Ark. Zool.* (2) **18**, 305–389.
- 1973. Weitere Fischreste aus dem Oberen Plattenkalk der Bergisch-Gladbach-Paffrather Mulde (Oberdevon, Rheinisches Schiefergebirge). *Palaeontographica*, **143A**, 159–187.
- 1980. Lower Devonian Porolepiformes from the Canadian Arctic with special reference to *Powichthys thorsteinsonni* Jessen. *Palaeontographica*, **167A**, 180–214.

- LAUDER, G. V. and LIEM, K. 1983. The evolution and interrelationships of the actinopterygian fishes. *Bull. Mus. comp. Zool. Harv.* **150**, 95–197.
- LONG, J. A. 1983. New bothriolepid fishes from the Late Devonian of Victoria, Australia. *Palaeontology*, **26**, 295–320.
- 1985a. The structure and relationships of a new osteolepiform fish from the Late Devonian of Victoria, Australia. *Alcheringa*, **9**, 1–22.
- 1985b. New information on the head and shoulder girdle of *Canowindra grossi* Thomson, from the Upper Devonian Mandagery Sandstone, New South Wales. *Recs. Aust. Mus.* **37**, 91–99.
- 1985c. A new osteolepidid fish from the Upper Devonian Gogo Formation, Western Australia. *Recs. West. Aust. Mus.* **12**, 361–377.
- 1985d. The evolution of the Crossopterygii: a study based on new material from the Devonian of Australia and Antarctica. (Abstract.) *Geol. Surv. New Zealand, Record*, **9**, 70–72.
- and TURNER, S. 1984. A checklist and bibliography of Australian fossil fishes. In ARCHER, M. and CLAYTON, G. (eds.). *Vertebrate Zoogeography and Evolution in Australasia*, 325–354. Hesperian Press, Perth.
- MARSDEN, M. A. H. 1976. Upper Devonian–Carboniferous. In DOUGLAS, J. and FERGUSON, J. (eds.). *Geology of Victoria. Geol. Soc. Aust. Spec. Pub.* **5**, 77–124.
- PANCHEN, A. L. 1973. On *Crassigyrinus scoticus* Watson, a primitive amphibian from the Lower Carboniferous of Scotland. *Palaeontology*, **16**, 179–193.
- 1985. On the amphibian *Crassigyrinus scoticus* Watson from the Carboniferous of Scotland. *Phil. Trans. R. Soc. B* **309**, 505–568.
- RACKOFF, J. S. 1980. The origin of the tetrapod limb and the ancestry of tetrapods. In PANCHEN, A. L. (ed.). *The Terrestrial Environment and the Origin of Land Vertebrates*, 255–92. Academic Press, London and New York.
- REED, A. 1975. *Aboriginal words and place names*. Rigby, Sydney.
- ROSEN, D. E., FOREY, P. L., GARDINER, B. G. and PATTERSON, C. 1981. Lungfish, tetrapods, palaeontology and plesiomorphy. *Bull. Am. Mus. nat. Hist.* **167**, 159–276.
- SCHULTZE, H.-P. 1970. Folded teeth and the monophyletic origin of the tetrapods. *Am. Mus. Novit.* **2408**, 1–10.
- and ARSENAULT, M. 1985. The panderichthyid fish *Elpistostege*: a close relative of tetrapods? *Palaeontology*, **28**, 293–309.
- THOMSON, K. S. 1973. Observations on a new rhipidistian fish from the Upper Devonian of Australia. *Palaeontographica*, **143A**, 209–220.
- VOROBYEVA, E. 1977. Morfologiya i osobennosti evolyutsii kisteperykh ryb. (Morphology and the nature of evolution of crossopterygian fish). *Trudy paleont. inst.*, Nauka, Moscow, **163**, 1–239.
- WOODWARD, A. S. 1906. On a Carboniferous fish fauna from the Mansfield District. *Mem. natn Mus. Vict.* **1**, 1–32.
- YOUNG, G. C. 1981. Biogeography of Devonian vertebrates. *Alcheringa*, **5**, 223–245.
- and GORTER, J. D. 1981. A new fish fauna of Middle Devonian age from the Taemas/Wee Jasper region of New South Wales. *Bull. Bur. Miner. Resour. Geol. Geophys. Aust.* **209**, 83–147.

J. A. LONG

Department of Geology
University of Western Australia
Nedlands
Western Australia 6009

Typescript received 4 September 1985

Revised typescript received 12 March 1987